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INTENSITY AND CHRONOLOGY OF POSTREPRODUCTIVE MOLTS IN MALE CANVASBACKS

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Abstract.—We studied molt intensity and chronology in male Canvasbacks (*Aythya valisineria*) from termination of reproductive activities until fall migration (May–October) in 1989–1990. During this period, male Canvasbacks underwent prebasic, down, and partial prealternate molts. Males arrived on molting habitat already undergoing light prebasic molt. Total molt intensity increased to moderate levels in late preflightless birds and remained at this intensity through the postflightless period. Contour plumage molt intensity was reduced in staging birds concurrent with declining ambient temperatures and fall migration. Prebasic body molt was most intense in late preflightless birds, while peak prealternate molt occurred during the postflightless period. Remigial molt occurred from late July through August near completion of prebasic body molt. Prealternate molt began concurrent with late remigial molt and was not completed in male Canvasbacks before fall migration from central Alberta. Synchrony in the timing of remigial and prealternate molts suggests that these molts were probably under photoperiodic regulation in male Canvasbacks. Down replacement occurred throughout the postreproductive period but reached peak intensity in late preflightless, flightless, and postflightless birds. Only light down molt still occurred in staging Canvasbacks. All male Canvasbacks examined underwent the normal progression of postreproductive molts regardless of age; however, yearling males initiated prebasic molt earlier than birds ≥2 years old. Male Canvasbacks extended postreproductive molts over a period of six months which minimized the daily nutritional requirements for plumage growth. *Received 21 Mar. 1994, accepted 10 Nov. 1994.*

Determining the intensity and chronology of molts in waterfowl (Anseriformes) is necessary to understand nutritional demands throughout the annual cycle. Molt is a productive process involving nutrient demands in addition to those for basal metabolic requirements, reproduction, and activity (King 1974). Nutrient requirements during molt arise primarily from an increased need for protein to meet the amino acid demands of epidermal keratin synthesis. Elevated energetic demands during molt originate from energy deposited in plumage and physiological processes (i.e., elevated somatic protein metabolism, alterations in water balance, increased blood volume, cyclic osteoporosis) that birds undergo to facilitate keratin synthesis (King 1980). Nutrient and energy demands in addition to those for plumage may originate from requirements for synthesis of feather sheaths, integument, and other epidermal structures replaced during molt (Murphy and King 1986, King and Murphy 1990).

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Male Canvasbacks (*Aythya valisineria*) molt primarily on large athalassic and subsaline wetlands in the aspen parklands and southern boreal forest regions of central and western Canada (Bergman 1973, Bailey 1983). During the postreproductive period, extending from termination of breeding activities until departure for fall migration, adult male Canvasbacks undergo prebasic, down, and partial prealternate molts. Little is known about the influence of molt intensity and chronology on nutritional requirements and timing of other energy demanding events (e.g., fall migration) during this period. Furthermore, most studies on molt in ducks (Anatinae) investigate only patterns of contour feather replacement and neglect down plumage molt. Our study reports intensity and chronology of feather replacement during prebasic, prealternate, and down molts in postreproductive male Canvasbacks molting in central Alberta. This research was conducted as part of a broader study that focused primarily on the nutritional tactics of Canvasbacks during molt (Thompson 1992).

STUDY AREA AND METHODS

Beaverhill Lake (53°27′N, 112°32′W) in the aspen parkland biome (Bird 1930, Strong and Leggat 1981) of east-central Alberta is traditionally used by molting and fall migrant Canvasbacks (Lister 1979). This large lacustrine wetland (Cowardin et al. 1979) covers approximately 139 km^2 in a shallow glacial depression with an average water depth of <1 m throughout most of the basin. The northeastern sector of Beaverhill Lake is a large delta-like marsh with expansive bays and extensive emergent macrophyte growth. Hardstem bulrush (*Scirpus acutus*) dominates deepwater marsh zones, with small stands of great bulrush (*S. validus*) occurring on shallower alkaline mud flats. Nearshore zones with lower alkalinity are dominated by cattail (*Typha* spp.). Submergent macrophyte growth generally begins 50–75 m from the lakeshore and varies markedly in distribution throughout the wetland. Sago pondweed (*Potamogeton pectinatus*), an important Canvasback food (Bartonek and Hickey 1969, Bergman 1973, Austin et al. 1990, Thompson 1992), is the dominant submersed aquatic plant forming large monotypic stands throughout the basin. Extensive pondweed beds occur in northern and southwestern regions of the lake and receive heavy use by molting and migrant waterfowl.

Male Canvasbacks (N = 143) were collected by shooting along traditionally used flight corridors and foraging sites from late May through October in 1989 and 1990. Additionally, some flightless birds were collected from a boat on calm days when they could be observed diving. Coloration of basic and alternate generations of contour plumage in male Canvasbacks were distinct in all tracts that underwent both molts (See descriptions in Palmer 1976) permitting reliable discrimination of stage of molt. Specimens were categorized into plumage classes using the following terminology and molt characteristics: (1) Early Preflightless (N = 32), early to intermediate stages of prebasic molt (≤50% basic plumage in capital and side-flank regions); (2) Late Preflightless (N = 28), advanced prebasic molt (> 50% basic plumage in capital and side-flank regions); (3) Flightless (N = 27), definitive basic plumage and incoming primaries and secondaries <80% of final length; (4) Postflightless (N = 29), early to intermediate stages of prealternate molt (≤50% alternate plumage in the capital and side-flank regions) and primaries and secondaries with sufficient growth for flight (>80% of mature length); and (5) Staging (N = 27), advanced prealternate molt (>50% alternate

TABLE 1

GENERAL CHRONOLOGY AND DURATION OF MOLT STAGES FOR ADULT MALE CANVASBACKS IN CENTRAL ALBERTA

	Year	
Molt stage	1989	1990
Early preflightless	21 May–29 June	22 May–2 July
Late preflightless	20 June–12 August	27 June–28 July
Flightless	22 July–6 September	23 July–5 September
Postflightless	26 August–22 September	27 August–24 September
Staging	21 September–14 October	24 September–19 October

plumage in capital and side-flank regions). General chronology and duration of molt stages were based on time budget observations (Thompson 1992) (Table 1).

Molt terminology follows that of Humphrey and Parkes (1959) except that remigial molt, which is part of prebasic molt, is discussed independently because of its significant nutrient requirements (Thompson 1992). Molt of down plumage is discussed separately because current molt terminology was developed exclusively from, and for description of, contour feather replacement patterns (See Humphrey and Parkes 1959). Each specimen was examined for contour plumage and down molt in 20 feather tracts comprising nine major plumage regions (Table 2). Separate scores of molt intensity were recorded for down and contour plumage in each tract. Plumage region and feather tract terminology were adapted from Billard and Humphrey (1972) and Titman et al. (1990).

Molt was detected by observing empty feather follicles and partially or fully ensheathed feathers (i.e., pinfeathers or blood quills). Molting contour and alar feathers were identified by presence of a vascularized calamus (Miller 1986). Incoming down feathers were distinguished from growing contour feathers by their small size and lack of a distinct basal calamus (Lovvorn and Barzen 1988). Distinction of molting feathers was most difficult in the capital region because of small contour and down plumage.

TABLE 2

ANATID PLUMAGE REGIONS AND THEIR CORRESPONDING FEATHER TRACTS[a]

Plumage regions	Feather tracts
Capital	Crown, facial, chin-throat, neck
Anterior ventral and spinal	Upper chest, upper back, center chest
Side-flank	Side chest, flanks
Scapular	Scapulars
Ventral	Belly
Posterior spinal	Lower back, rump
Tail coverts	Upper tail coverts, lower tail coverts
Rectrix	Rectrices
Wing	Primaries, secondaries, tertials, wing coverts

[a] Adapted from Billard and Humphrey (1972) and Titman et al. (1990).

Scoring of molt was done externally to minimize damage to tissues used in subsequent carcass composition analyses (Thompson 1992). All tracts were examined for contour plumage and down molt using the technique described by Greenwood et al. (1983). Each tract was scored using the following designations based on estimation of percent occurrence of pinfeathers: 0 = no molt, 1 = light molt (1–15% pinfeathers), 2 = intermediate molt (>15–40% pinfeathers), and 3 = heavy molt (> 40% pinfeathers). A mean regional, tract, or total molt score of 0 indicated absence of molt; 0.01–1.00 light molt; 1.01–2.00 intermediate molt; and 2.01–3.00 heavy molt. It should be noted that in the following discussion, peak seasonal molt intensity does not necessarily correspond with heavy molt intensity but instead represents the highest molt intensity observed in a given plumage region or feather tract during the postreproductive period.

Molt scores within plumage regions were calculated by summing scores of all feather tracts within a region and dividing by the number of regional subdivisions. Total molt scores were derived by averaging the nine regional molt scores. Nonparametric statistical procedures were used for data analysis because molt scores frequently exhibited bimodal or skewed distributions and heterogeneity of variances. Differences in molt intensity between plumage classes were determined using Kruskal-Wallis one-way analysis of variance tests (PROC NPAR1WAY; SAS Institute 1985). If significant variation ($P < 0.05$) occurred in the overall model, contrasting plumage classes were determined using Dunn's multiple comparisons test (Daniel 1990).

RESULTS AND DISCUSSION

Contour feather molt intensity.—Mean tract, regional, and total molt scores for each plumage class are presented in Table 3. Molt intensity data from 1989 and 1990 were pooled due to lack of variation ($P > 0.05$, Kruskal-Wallis ANOVA) between years in regional and total molt scores. Conversely, all plumage regions and feather tracts exhibited significant ($P < 0.05$) variation in mean molt intensity between plumage classes except for the facial tract ($H = 6.99$, $P = 0.14$). Age-related differences in molt intensity among adult male Canvasbacks (≥2 years old) were not apparent, since birds in this age class were undergoing definitive molt cycles (Palmer 1976). Only seven yearling males were collected when molting from Alternate I into definitive basic plumage. These specimens were consistently in advanced prebasic molt relative to older birds suggesting earlier initiation of this complete molt in yearling males.

Total molt score: Molt intensity increased from the early preflightless to the late preflightless period as prebasic body molt advanced (Table 3). Molt intensity remained elevated during the flightless and postflightless periods while birds were undergoing overlapping periods of prebasic and prealternate molts. Molt intensity declined from the postflightless to the staging period as prealternate molt was completed or reduced in many feather tracts (Table 3).

Early preflightless: Canvasbacks in this molt stage exhibited molt in all plumage regions indicating rapid progression of prebasic body molt as reproductive activities subsided. Prebasic molt in the capital, side-flank,

TABLE 3

MEAN MOLT SCORES IN THE PLUMAGE REGIONS AND FEATHER TRACTS OF POSTREPRODUCTIVE MALE CANVASBACKS MOLTING IN CENTRAL ALBERTA

	Molt status effects		Molt periods[a]								
Feather regions and tracts	H^b	$P > H^c$	EP (32)[d]	P^e	LP (28)	P	FL (27)	P	PF (29)	P	ST (27)
Capital	12.11	0.02	1.66 (0.06)[f]	NS	1.60 (0.06)	NS	1.43 (0.07)	**	1.71 (0.06)	*	1.45 (0.08)
Crown	12.62	0.01	1.90 (0.07)	NS	1.70 (0.09)	NS	1.46 (0.10)	NS	1.69 (0.09)	NS	1.55 (0.09)
Facial	6.99	0.14	1.50 (0.09)	NS	1.53 (0.09)	NS	1.39 (0.09)	NS	1.63 (0.09)	NS	1.28 (0.11)
Chin–throat	17.36	0.0016	1.63 (0.09)	NS	1.40 (0.09)	NS	1.64 (0.09)	NS	1.91 (0.05)	*	1.62 (0.09)
Neck	23.37	0.0001	1.60 (0.09)	NS	1.77 (0.08)	***	1.21 (0.08)	**	1.63 (0.09)	NS	1.34 (0.09)
Side-flank	69.41	0.0001	2.00 (0.07)	***	2.52 (0.06)	***	1.50 (0.08)	***	2.55 (0.06)	NS	2.34 (0.08)
Side chest	72.63	0.0001	1.29 (0.11)	***	2.26 (0.11)	***	1.52 (0.10)	***	2.78 (0.07)	***	2.00 (0.12)
Flanks	63.94	0.0001	2.71 (0.08)	NS	2.77 (0.08)	***	1.48 (0.11)	***	2.31 (0.08)	*	2.69 (0.09)
Anterior ventral and spinal	59.27	0.0001	1.16 (0.11)	***	2.11 (0.08)	***	1.41 (0.08)	***	1.98 (0.04)	NS	1.79 (0.07)
Upper back	31.50	0.0001	1.31 (0.13)	**	1.94 (0.11)	***	1.21 (0.08)	NS	1.17 (0.07)	*	1.55 (0.09)
Upper chest	22.17	0.0002	1.31 (0.18)	**	2.13 (0.17)	**	1.33 (0.13)	*	1.85 (0.10)	NS	2.00 (0.10)
Center chest	77.63	0.0001	0.97 (0.11)	***	2.29 (0.11)	**	1.65 (0.12)	***	2.83 (0.07)	***	1.93 (0.13)

TABLE 3
CONTINUED

Feather regions and tracts	Molt status effects		Molt periods[a]								
	H[b]	$P > H$[c]	EP (32)[d]	P[e]	LP (28)	P	FL (27)	P	PF (29)	P	ST (27)
Ventral (belly)	82.69	0.0001	1.23[f] (0.08)	***	1.97 (0.07)	**	1.39 (0.09)	***	2.72 (0.08)	***	1.68 (0.10)
Scapular	65.63	0.0001	2.52 (0.09)	NS	2.74 (0.08)	***	1.67 (0.09)	NS	1.94 (0.06)	NS	2.18 (0.07)
Posterior spinal	72.78	0.0001	0.84 (0.08)	***	1.55 (0.09)	NS	1.82 (0.09)	NS	2.05 (0.07)	*	1.76 (0.07)
Lower back	67.98	0.0001	0.76 (0.09)	***	1.53 (0.09)	*	2.07 (0.13)	NS	1.94 (0.08)	**	1.41 (0.10)
Rump	68.99	0.0001	0.91 (0.09)	***	1.57 (0.10)	NS	1.55 (0.09)	**	2.16 (0.11)	NS	2.11 (0.06)
Rectrix (rectrices)	80.19	0.0001	0.39 (0.09)	***	1.23 (0.18)	***	2.68 (0.10)	***	1.16 (0.10)	NS	0.98 (0.13)
Tail covert	48.01	0.0001	1.65 (0.12)	*	2.12 (0.12)	***	1.52 (0.08)	***	2.52 (0.07)	**	2.04 (0.09)
Upper tail coverts	40.44	0.0001	1.51 (0.12)	*	2.00 (0.13)	***	1.29 (0.09)	***	2.26 (0.09)	**	1.63 (0.11)
Lower tail coverts	36.53	0.0001	1.79 (0.18)	NS	2.23 (0.13)	*	1.75 (0.11)	***	2.77 (0.08)	NS	2.44 (0.11)
Wing	93.76	0.0001	0.01 (0.01)	*	0.14 (0.03)	***	2.66 (0.05)	***	0.25 (0.05)	NS	0.11 (0.03)
Primaries	112.10	0.0001	0.00 (0.00)	NS	0.00 (0.00)	***	3.00 (0.00)	***	0.50 (0.11)	NS	0.24 (0.08)

TABLE 3
CONTINUED

Feather regions and tracts	Molt status effects		Molt periods[a]								
	H[b]	$P > H$[c]	EP (32)[d]	P[e]	LP (28)	P	FL (27)	P	PF (29)	P	ST (27)
Secondaries	144.94	0.0001	0.00[f] (0.00)	NS	0.00 (0.00)	***	3.00 (0.00)	***	0.00 (0.00)	NS	0.00 (0.00)
Tertials	103.13	0.0001	0.03 (0.03)	NS	0.38 (0.10)	***	2.86 (0.07)	***	0.20 (0.07)	NS	0.14 (0.07)
Wing coverts	97.81	0.0001	0.03 (0.03)	NS	0.14 (0.07)	***	1.75 (0.16)	***	0.30 (0.09)	NS	0.07 (0.05)
Total molt score	62.90	0.0001	1.21 (0.06)	***	1.78 (0.04)	NS	1.80 (0.05)	NS	1.87 (0.02)	**	1.68 (0.05)

[a] Molt periods include early preflightless (EP), late preflightless (LP), flightless (FL), postflightless (PF), and staging (ST).
[b] Kruskal-Wallis test statistic.
[c] Overall probability from Kruskal-Wallis test that molt scores differ by stage of molt.
[d] Sample size.
[e] Probability from Dunn's multiple comparisons test that adjacent means differ by chance; * = $P \leq 0.05$, ** = $P \leq 0.01$, *** = $P \leq 0.001$, NS = $P > 0.05$.
[f] Standard error of mean.

scapular, and tail covert regions of male Canvasbacks was initiated late in the breeding season as nearly all birds arriving on molting habitat exhibited some degree of molt in these regions. Lovvorn and Barzen (1988) recorded low intensity prebasic molt in capital and body tracts of breeding male Canvasbacks in Manitoba, but the exact locations of molt within these regions were not reported. Capital and scapular regions reached peak prebasic molt intensity in early preflightless Canvasbacks, whereas wing, rectrix, and posterior spinal regions showed only light, sporadic molt.

Late preflightless: Intensity of prebasic molt increased from the early preflightless period in the side-flank, anterior ventral and spinal, ventral, posterior spinal, rectrix, tail covert, and wing regions of late preflightless Canvasbacks (Table 3). Feather replacement intensity was typically similar within plumage regions, but most molting feathers in the side-flank region occurred in the side chest tract. Capital tracts molted at moderate intensity, and scapulars continued to molt heavily as observed in early preflightless birds. Anterior ventral and spinal, ventral, and tail covert regions reached the maximum prebasic molt intensity. The capital, ventral, posterior spinal, and rectrix regions had moderate molt intensity, while the side-flank, anterior ventral and spinal, scapular, and tail covert regions molted heavily. Only the wing region maintained light prebasic molt intensity in late preflightless Canvasbacks.

Flightless: Canvasbacks in this period reduced molt intensity from the late preflightless period in the side-flank, ventral, anterior ventral and spinal, scapular, and tail covert regions as prebasic body molt was completed (Table 3). Capital molt intensity remained unchanged from late preflightless levels but decreased ($P < 0.05$) in comparison to early preflightless molt intensity. During intermediate to late remigial growth, prealternate molt was initiated in the capital region and flanks. Overall, the posterior spinal region maintained similar molt intensity to late preflightless levels; however, one regional subdivision, the lower back tract, increased prebasic molt intensity (Table 3). Capital, ventral, and posterior spinal regions continued to molt at moderate levels similar to late preflightless birds, while the side-flank, anterior ventral and spinal, scapular, and tail covert regions decreased from heavy molt intensity during the late preflightless period to moderate levels in flightless birds (Table 3). Wing and rectrix regions reached peak prebasic molt intensity in flightless birds as all feather tracts in these plumage regions molted heavily.

Postflightless: Following remigial molt, Canvasbacks initiated extensive prealternate molt in the capital, side-flank, anterior ventral and spinal, ventral, and tail covert regions. Intensity of prealternate molt was greatest in the neck, flanks, side chest, upper chest, center chest, and upper and lower tail covert feather tracts. Detection of both prebasic and prealternate molt in the tail covert region was possible because these tracts were designated as a separate region from the rectrices which are replaced only once per plumage cycle during prebasic molt in pochards (i.e., members of the genus *Aythya*) (Palmer 1976). Some molt studies have erroneously included the rectrices and tail coverts in a single plumage region (see Austin and Fredrickson 1986) thereby grouping tracts with inherently different molt patterns. Overlap in completion of prebasic molt and initiation of prealternate molt in the scapular region masked detection of increased molt intensity in this region. The posterior spinal region showed no change in overall molt intensity from the flightless period; however, the rump tract showed increased prebasic molt intensity (Table 3). Rectrix and wing molt declined markedly from the flightless to the postflightless period as prebasic molt neared completion in these regions (Table 3).

Staging: Prealternate molt intensity declined from the postflightless period in the capital, ventral, and tail covert regions of staging Canvasbacks (Table 3). Within these regions, prealternate molt intensity declined significantly from postflightless levels in the chin-throat, belly, and upper tail coverts (Table 3). Molt intensity remained unchanged from postflightless levels in the side-flank, anterior ventral and spinal, scapular, rectrix, and wing regions. Tracts within the anterior ventral and spinal region did not molt consistently during the staging period; the upper back tract increased prealternate molt intensity, while feather replacement declined in the center chest tract (Table 3). Acquisition of alternate scapulars in male Canvasbacks occurs gradually despite high molt intensity in staging birds and is not completed until later in fall migration or early winter (Lovvorn and Barzen 1988). Wing molt persisted only at negligible levels as primaries and tertials completed maturation.

Down molt intensity.—Mean down molt scores for plumage regions and tracts are presented in Table 4. Down plumage was replaced only once in male Canvasbacks during the postreproductive period. Only negligible down molt occurs outside the postbreeding period (Lovvorn and Barzen 1988), indicating that down is replaced only once annually in male Canvasbacks. Male Redheads (*Aythya americana*) also replace down plumage once per year concurrent with late prebasic and early prealternate molt (Bailey 1982).

Total down molt score: Replacement of down plumage increased from light intensity in the early preflightless period to moderate intensity in the late preflightless period (Table 4). Male Canvasbacks maintained moderate levels of down replacement from the late preflightless period through the postflightless period. Molt intensity declined to low levels in staging birds as down molt neared completion before fall migration (Table 4).

TABLE 4

MEAN DOWN MOLT SCORES IN THE PLUMAGE REGIONS AND FEATHER TRACTS OF POSTREPRODUCTIVE MALE CANVASBACKS MOLTING IN CENTRAL ALBERTA

Feather regions and tracts	Molt status effects		Molt periods[a]								
	H[b]	$P > H$[c]	EP (32)[d]	P[e]	LP (28)	P	FL (27)	P	PF (29)	P	ST (27)
Capital	39.90	0.0001	0.70 (0.13)[f]	*	1.13 (0.07)	NS	1.67 (0.16)	NS	1.39 (0.06)	***	0.40 (0.07)
Crown	30.10	0.0001	0.80 (0.14)	NS	1.23 (0.12)	NS	1.80 (0.20)	NS	1.64 (0.13)	***	0.50 (0.15)
Facial	43.15	0.0001	0.47 (0.13)	*	1.00 (0.11)	NS	1.40 (0.13)	NS	1.14 (0.10)	***	0.00 (0.00)
Chin–throat	27.48	0.0001	0.87 (0.19)	NS	1.15 (0.10)	NS	1.60 (0.16)	NS	1.29 (0.13)	***	0.25 (0.13)
Neck	24.55	0.0001	0.67 (0.13)	NS	1.15 (0.15)	NS	1.87 (0.24)	NS	1.50 (0.14)	*	0.83 (0.11)
Side-flank	36.41	0.0001	0.97 (0.14)	**	1.67 (0.09)	NS	1.79 (0.13)	*	1.25 (0.10)	**	0.62 (0.10)
Side chest	30.40	0.0001	1.35 (0.21)	**	2.33 (0.14)	NS	2.50 (0.17)	*	1.71 (0.13)	NS	1.08 (0.18)
Flanks	25.02	0.0001	0.59 (0.12)	NS	1.00 (0.12)	NS	1.07 (0.13)	NS	0.79 (0.11)	**	0.15 (0.10)
Anterior ventral and spinal	41.82	0.0001	1.00 (0.15)	***	2.02 (0.13)	NS	1.76 (0.09)	**	1.25 (0.04)	NS	0.67 (0.13)
Upper back	25.40	0.0001	0.93 (0.15)	*	1.57 (0.17)	NS	1.50 (0.14)	NS	1.08 (0.08)	*	0.47 (0.17)
Upper chest	37.21	0.0001	1.00 (0.17)	***	2.21 (0.19)	*	1.43 (0.17)	*	1.00 (0.00)	NS	0.47 (0.13)
Center chest	24.25	0.0001	1.07 (0.27)	***	2.29 (0.16)	NS	2.36 (0.20)	NS	1.69 (0.13)	NS	1.27 (0.18)

TABLE 4
CONTINUED

Feather regions and tracts	Molt status effects		Molt periods[a]								
	H[b]	$P > H$[c]	EP (32)[d]	P[e]	LP (28)	P	FL (27)	P	PF (29)	P	ST (27)
Ventral (belly)	36.92	0.0001	1.36 (0.13)[f]	***	2.54 (0.14)	NS	2.43 (0.14)	**	1.53 (0.13)	NS	1.07 (0.21)
Scapular	34.87	0.0001	0.71 (0.11)	NS	0.62 (0.14)	*	1.23 (0.12)	NS	1.40 (0.13)	***	0.15 (0.10)
Posterior spinal	39.38	0.0001	1.17 (0.06)	NS	1.46 (0.16)	***	2.36 (0.12)	NS	2.13 (0.09)	***	1.25 (0.14)
Lower back	27.45	0.0001	1.27 (0.12)	NS	1.57 (0.20)	**	2.43 (0.17)	NS	1.87 (0.09)	*	1.14 (0.18)
Rump	40.66	0.0001	1.07 (0.07)	NS	1.36 (0.17)	**	2.29 (0.13)	NS	2.40 (0.16)	***	1.36 (0.13)
Rectrix (rectrices)	41.39	0.0001	0.13 (0.09)	**	0.86 (0.14)	NS	1.27 (0.18)	NS	1.47 (0.13)	***	0.29 (0.13)
Tail covert	24.36	0.0001	1.03 (0.12)	***	1.96 (0.19)	NS	1.57 (0.13)	NS	1.20 (0.08)	NS	1.04 (0.13)
Upper tail coverts	21.09	0.0003	1.00 (0.09)	**	1.86 (0.23)	NS	1.47 (0.13)	NS	1.07 (0.07)	NS	1.00 (0.10)
Lower tail coverts	17.38	0.0016	1.06 (0.19)	**	2.07 (0.20)	NS	1.67 (0.19)	NS	1.33 (0.16)	NS	1.07 (0.22)
Wing	58.28	0.0001	0.00 (0.00)	**	1.02 (0.12)	***	2.48 (0.09)	NS	1.94 (0.15)	***	0.50 (0.14)
Primaries	56.82	0.0001	0.00 (0.00)	**	1.08 (0.18)	**	2.87 (0.09)	*	1.62 (0.18)	**	0.25 (0.18)

TABLE 4
CONTINUED

Feather regions and tracts	Molt status effects		Molt periods[a]								
	H[b]	$P > H$[c]	EP (32)[d]	P[e]	LP (28)	P	FL (27)	P	PF (29)	P	ST (27)
Secondaries	56.74	0.0001	0.00[f]	**	1.08	**	2.67	NS	1.92	***	0.17
			(0.00)		(0.18)		(0.13)		(0.21)		(0.11)
Tertials	52.54	0.0001	0.00	**	1.08	**	2.47	NS	2.23	**	0.75
			(0.00)		(0.14)		(0.13)		(0.17)		(0.25)
Wing coverts	42.66	0.0001	0.00	*	0.85	**	1.93	NS	2.00	**	0.83
			(0.00)		(0.19)		(0.18)		(0.23)		(0.27)
Total down molt score	49.78	0.0001	0.81	**	1.50	NS	1.84	NS	1.49	***	0.65
			(0.07)		(0.04)		(0.08)		(0.06)		(0.08)

[a] Molt periods include early preflightless (EP), late preflightless (LP), flightless (FL), postflightless (PF), and staging (ST).
[b] Kruskal-Wallis test statistic.
[c] Overall probability from Kruskal-Wallis test that molt scores differ by stage of molt.
[d] Sample size.
[e] Probability from Dunn's multiple comparisons test that adjacent means differ by chance; * = $P \leq 0.05$, ** = $P \leq 0.01$, *** = $P \leq 0.001$, NS = $P > 0.05$.
[f] Standard error of mean.

Lovvorn and Barzen (1988) indicated that down molt is complete in adult male Canvasbacks late in fall migration.

Early preflightless: Down molt began in all plumage regions except for the wings of early preflightless Canvasbacks. Molt was light in most regions except for the ventral, posterior spinal, and tail covert regions which had moderate molt intensity. Despite low overall levels of down replacement in the side-flank region, the side chest tract had moderate molt intensity, and reflected a pattern of down molt similar to the ventral region. Because down molt does not necessarily coincide with contour feather molt in designated feather tracts, it is probable that a better grouping of down plumage regions not based on contour feather location could be devised.

Late preflightless: Down molt increased from the early preflightless period in capital, side-flank, anterior ventral and spinal, ventral, rectrix, tail covert, and wing regions of late preflightless Canvasbacks (Table 4). Increased molt intensity represented peak seasonal down replacement in all regions except for the scapular, posterior spinal, and wing tracts. Average down molt scores were typically higher in flightless birds than late preflightless birds, but variation in molt intensity between plumage classes masked detection of significant differences. Only molt in scapular and posterior spinal regions remained unchanged from early preflightless levels. Molt intensity in most plumage regions proceeded at moderate levels except for the anterior ventral and spinal and ventral regions that were undergoing heavy down replacement. Only the scapular and rectrix regions still maintained light down molt intensity.

Flightless: Down molt continued at levels similar to late preflightless birds in the capital, side-flank, anterior ventral and spinal, ventral, rectrix, and tail covert regions of flightless Canvasbacks. Down molt increased to peak seasonal levels in the scapular, posterior spinal, and wing regions during remigial molt (Table 4). All plumage regions of flightless birds had moderate down molt intensity, with exception of the ventral, posterior spinal, and wing regions which were undergoing heavy levels of down replacement.

Postflightless: Intensity of down molt remained unchanged from flightless levels in the capital, scapular, posterior spinal, rectrix, tail covert, and wing regions of postflightless Canvasbacks. Patterns of molt within tracts of the wing region were not consistent because intensity of down replacement near the primaries decreased from flightless levels. The extent of down molt also declined from flightless birds in the side-flank, anterior ventral and spinal, and ventral regions (Table 4). Reduced molt intensity in the side-flank and anterior ventral and spinal regions was due primarily to diminished down replacement in the side chest and upper chest tracts, respectively.

Staging: Canvasbacks in this plumage class had reduced down molt intensity in capital, side-flank, scapular, posterior spinal, rectrix, and wing regions in comparison to postflightless birds (Table 4). Down molt was similar within regions except for the side chest tract which maintained consistent down molt intensity despite an overall decrease in molt within the side-flank region from the postflightless period (Table 4). Molt of down plumage continued at similar levels in postflightless and staging birds in the anterior ventral and spinal, ventral, and tail covert regions. Replacement of down decreased in the upper back tract despite the lack of regional change in molt intensity in anterior ventral and spinal plumage (Table 4). Light down molt continued throughout the staging period in the capital, side-flank, anterior ventral and spinal, scapular, rectrix, and wing regions, while moderate molt intensity was maintained in the ventral, posterior spinal, and tail covert tracts. Staging male Canvasbacks had not completed down molt before fall migration from central Alberta.

Chronology and pattern of prebasic molt.—Prebasic molt in male Canvasbacks extended from mid-May through September and was a complete molt because head, body, rectrix, and remigial plumage was replaced. Male Canvasbacks initiate prebasic molt late in the breeding season (Lovvorn and Barzen 1988). Feather replacement begins in capital tracts, followed by scapulars, flanks, and tail coverts. Only the posterior spinal tracts continued prebasic molt into October in postflightless and staging Canvasbacks. The timing of prebasic molt in the posterior spinal region of male pochards is misleading, causing some researchers to consider it as prealternate molt (see Bailey 1982). Because feather follicles in the posterior spinal region are activated only once during the annual molt cycle, feathers of the lower back and rump tracts should be considered basic plumage (Humphrey and Parkes 1959, Palmer 1972) in male pochards.

Chronology of prebasic body molt varies with age in male Canvasbacks. Yearling males which had probably neither been paired nor participated in breeding activities arrived on molting areas first, often in advanced prebasic molt. Older males, which presumably had a more extended breeding effort, arrived on molting sites later, with only light prebasic molt in capital and side-flank regions. Breeding male Redheads began prebasic molt earlier in a year with abbreviated or no reproductive effort (Bailey 1982). During years with extended breeding seasons, prebasic body molt was temporally compressed in male Redheads before remigial molt.

Hochbaum (1944) suggested that variation in onset of prebasic molt in male Canvasbacks was related to the bird's prior breeding status. He observed among captive birds that feather replacement began first in the earliest breeding males, followed by males paired to the latest nesting females, and finally nonbreeding males (typically yearlings), a sequence different from that which we observed in wild birds. Initiation sequence of prebasic molt among male ducks in several other species (Oring 1968, Palmer 1972, Bailey 1982) supports the pattern of molt progression we observed in wild Canvasbacks in that feather replacement was initiated first in yearling males which had probably not bred, followed by older, previously paired males. Hochbaum (1944) also suggested from his captive studies that male Canvasbacks >3 years old underwent only partial prebasic molt, with some birds molting directly from alternate to alternate head-body plumage. Most of the birds examined during our study were adult males, including many drakes that were at least three years old as determined by wing plumage characteristics (Serie et al. 1982). All specimens from this older age cohort underwent a normal progression of post-reproductive molts and did not skip or undergo reduced prebasic molt as suggested by Hochbaum (1944). Studies of molt using captive Canvasbacks may have limited generalization to wild birds. Palmer (1972) warned that captivity can alter timing and duration of molt in waterfowl and that observations from captive birds should be considered speculative.

Most prebasic body molt was completed before male Canvasbacks shed their remiges or during early remigial growth. The posterior spinal region tracts, including the lower back and rump, were notable exceptions, with prebasic molt continuing through fall staging in October. Many feather tracts, particularly those in the capital and side-flank regions, initiated prealternate molt almost immediately upon completion of prebasic molt.

Chronology and pattern of prealternate molt.—Prealternate molt in male Canvasbacks began before completion of remigial molt and was an incomplete molt because the basic wing, rectrices, and plumage of the posterior spinal region were retained. Male Canvasbacks initiated prealternate molt when primaries were approximately 40% mature. There was a high degree of synchrony in onset of prealternate molt, suggesting photoperiodic regulation of this body molt in adult male Canvasbacks (see postflightless birds in Table 1). Feather replacement was first apparent in capital and side-flank regions in late August while birds were still flightless, but peak prealternate molt occurred in most plumage regions during the postflightless period in September when remigial growth was near completion. Scapulars were the last feathers to undergo prealternate molt, with peak replacement occurring during premigratory staging (Table 3). Low intensity molt in the scapulars of male Canvasbacks continues throughout winter, increasing again in February, particularly in juveniles (Lovvorn and Barzen 1988).

Hochbaum (1944) suggested that some male Canvasbacks attained definitive alternate plumage by September. Hochbaum's conclusion may have been based on observation of birds at a distance that appeared to be in full alternate plumage in late September, but if examined more closely would likely have been undergoing various stages of prealternate molt. In fact, none of the birds we examined had completed prealternate molt even by late October. Prealternate molt is apparently not complete in adult male Canvasbacks until late fall migration in November (Lovvorn and Barzen 1988) which is earlier than in male Greater Scaup (*Aythya marila*) that do not attain definitive alternate plumage until late December (Billard and Humphrey 1972). In both species, adult males complete prealternate molt before juveniles (Billard and Humphrey 1972, Lovvorn and Barzen 1988).

Chronology and pattern of remigial molt and rectrix replacement.— Wing molt in male Canvasbacks began in the tertial tract as reported for male Gadwalls (Oring 1968). Some tertial molt occurred in early and late preflightless Canvasbacks, but most tertials did not molt until the flightless stage. The innermost tertials were replaced during both prebasic and prealternate molts in Canvasbacks as reported by Palmer (1976). Replacement of basic tertials began late in the postreproductive period and was completed by January (Lovvorn and Barzen 1988).

The earliest molting male Canvasbacks initiated wing molt in late July during both years of this study (Table 1). However, the peak number of flightless birds occurred consistently during the second week of August when 90% of males were undergoing remigial molt. Synchrony in timing of remigial molt in successive years indicated strong photoperiodic control of this molt in male Canvasbacks. Some male Canvasbacks were still flightless as late as the first week of September, but most males (88%) had regained flight by this time. Hochbaum (1944) reported that male Canvasbacks underwent remigial molt on Lake Manitoba from late July to late August, during the same period as birds in this study.

Primaries and secondaries of male Canvasbacks were lost in close synchrony. Several flightless drakes collected early in remigial molt still possessed several intact flight feathers despite the absence of most others. All remiges still present were easily removed indicating that they were close to being shed. Proximal remiges, including the secondaries and inner primaries of Canvasbacks, matured more rapidly than distal primaries, permitting flight at earlier stages of remigial growth. Similar patterns of remigial maturation occur in other ducks (Weller 1957, Oring 1968, Bailey 1982, Young and Boag 1981, Austin and Fredrickson 1986).

Field observations in central Alberta indicated that male Canvasbacks were flightless for a period of three to four weeks. Canvasbacks in Manitoba had a similar flightless period of two and one-half to four weeks (Hochbaum 1944). Other male pochards, including Redheads (Bailey 1982) and Ring-necked Ducks (*Aythya collaris*) (Mendall 1958) also have a 3–4 week flightless period in the wild.

Wing coverts were the last alar tract to be replaced in male Canvasbacks. Most lesser and median coverts were not replaced until remigial growth was 40% complete. However, greater primary and secondary coverts were lost shortly after emergence of remiges, as observed in male Redheads (Bailey 1982). Replacement of ventral wing coverts, including the axillars, occurred primarily during latter remigial growth. Maturation of axillars was not complete in several postflightless and staging birds we examined, accounting for the light molt intensity in the wing covert tract during these periods (Table 3). Molt of the dorsal lesser and median wing coverts was quite variable, with some birds replacing feathers in these tracts simultaneously; however, most birds retained a heterogeneous mixture of growing and old coverts. Gradual replacement of wing coverts may provide some degree of protection to the wing and small fragile blood quills of maturing coverts.

Male Canvasbacks replace their rectrices once per plumage cycle, primarily during the flightless period. However, rectrix molt was observed throughout the postreproductive season, increasing in intensity from the early preflightless period to peak feather replacement during remigial molt and then steadily declining through fall staging (Table 3). Most rectrix replacement was complete in adult male Canvasbacks before fall migration from central Alberta.

Other anatids have similar irregular patterns of rectrix replacement during the postreproductive period. Wishart (1985) reported that the timing of rectrix replacement in male American Wigeons (*Anas americana*) was inconsistent, but central tail feathers were typically replaced first. Male Mallards (*Anas platyrhynchos*) initiated rectrix molt before remigial molt and continued tail feather replacement until fall migration (Young and Boag 1981). Tail molt in male Common Mergansers (*Mergus merganser*) (Erskine 1971) and female Lesser Scaup (*Aythya affinis*) (Austin and Fredrickson 1986) has also been described as prolonged and irregular following the breeding season.

Chronology and pattern of down plumage molt.—Down molt began in early preflightless Canvasbacks but did not reach peak intensity until the late preflightless period (Table 4). Down plumage replacement occurs more gradually than contour feather molts in male Canvasbacks, similar to the pattern of down replacement in male Mallards (Young and Boag

1981). Most down is replaced during late prebasic and early prealternate contour feather molts (late July–early September) in flightless male Canvasbacks. Mallards (Young and Boag 1981) and Redheads (Bailey 1982) also replace most of their down plumage during the flightless period in late summer before onset of cooler water and ambient temperatures. Down molt declined in staging Canvasbacks, but was not complete before fall migration in late October. Lovvorn and Barzen (1988) reported low levels of down molt continuing through fall in male Canvasbacks but negligible down molt by early winter.

Energetic aspects of postreproductive molts.—The adaptiveness of the ephemeral basic head-body plumage in male Canvasbacks is less apparent than the alternate generation which serves a strong function in mate selection. Furthermore, it is difficult to argue that basic plumage of male Canvasbacks makes them more cryptic during the flightless period because birds occupy open water habitats during remigial molt, making them readily visible (Thompson 1992). It is much easier to envision the survival advantage of drab colored basic plumage in male dabbling ducks which typically undergo wing molt in heavily vegetated marsh habitats where camouflage reduces detection by potential predators. Bailey (1982) suggested that the time basic plumage was worn by male Redheads served as a buffer period to ensure higher quality alternate plumage during spring courtship and breeding activities. Therefore, basic plumage was viewed as a transitional generation that delayed acquisition of alternate plumage, thereby reducing wear on the plumage that serves an epigamic role later in the annual cycle.

The higher quality alternate head-body plumage (Wielicki 1986) provides insulation for birds during the colder periods of the annual cycle and functions in epigamic display (Weller 1967). Male Canvasbacks may acquire alternate plumage far in advance of pairing because of the energetic advantage of undergoing extensive body molt during a warmer period of the year. If prealternate molt was delayed until late winter, just before onset of spring courtship, increased thermoregulatory costs from heat loss through blood-filled pinfeathers might be too great an energetic burden to incur concurrently with other energy requirements for maintenance and spring migration. Furthermore, the more vivid and bolder alternate plumage of older male Canvasbacks may function to establish dominance in large wintering aggregations within which individuals compete for optimal feeding locations (Alexander and Hair 1977).

Male Canvasbacks minimized per diem nutrient demands for plumage growth by extending the duration of postreproductive molts over six months. Low daily nutritional requirements for epidermal keratin synthesis allowed overlap in the timing of prebasic body molt and molt migration in the early preflightless period, both prebasic and prealternate body molts and down molt with remigial molt in flightless birds, and prealternate molt with fall migration in staging Canvasbacks. Similarly, female Canvasbacks continued prebasic body and down molts concurrent with spring migration and rapid follicular growth (Lovvorn and Barzen 1988).

Heitmeyer (1987) suggested that molt in anatids was timed to minimize or prevent overlap with other energy demanding events (e.g., migration and reproduction) in the annual cycle. However, this hypothesis presumes that daily nutritional requirements for molt are too high to sustain feather growth during other periods of elevated energy demands. By extending the duration of molt, birds can reduce daily nutritional requirements for plumage synthesis to the extent that temporal separation of molt from other energy demanding events in the annual cycle may not be necessary. Plumage growth concurrent with reproduction and migration in male and female Canvasbacks indicates that temporal overlap of molt and other energy demanding processes can occur in anatids with extended molt periods and low per diem nutritional requirements for molt.

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